Successional dynamics after pest eradication in the Karori Wildlife Sanctuary

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Abstract

We quantified the abundance, species richness and species composition of three size classes of native woody plants before and a decade after mammal eradication in the Karori Wildlife Sanctuary. Inventories were made in two large plots, one of which was located in introduced pine forest and the other was located in an area free from pines. Results were used to evaluate changes in forest structure following mammal exclusion. Smaller tree size classes increased in abundance through time in both plots. After controlling for the effect of plant abundances on estimates of species richness, few differences in species richness were observed between plots or sampling times. However, strong differences in species composition were observed. Different suites of tree species inhabited each plot. Nevertheless, species composition changed in similar ways in both plots through time. Overall results indicate that in the decade following mammal exclusion at the Karori Wildlife Sanctuary, 1) seedling abundances increased markedly, 2) species richness remained largely unchanged, and 3) species composition changed markedly through time, but in similar ways in both plots. Results indicate that complex successional changes have occurred in the Karori Wildlife Sanctuary since mammal eradication.

Key words: forest dynamics - introduced mammals - restoration - succession.

Introduction

Introduced mammals have had a dramatic effect on the ecology of New Zealand. The Karori Wildlife Sanctuary (KWS) is an ambitious attempt to restore wildlife threatened by introduced mammals to the New Zealand 'mainland'. It is a 252 ha section of regenerating forest on the outskirts of Wellington that was enclosed by a mammal-proof fence in 1995 (Campbell-Hunt 2002). All mammalian pests were eradicated within its boundaries, and over the past decade a variety of threatened animal species, such as little spotted kiwi (*Apteryx owenii*) and North Island robin (*Petroica australis*) have been relocated into its boundaries.

Introduced mammals not only affect native fauna (Wilson 2004), but they can also negatively impact the native New

Zealand flora. Efforts to better understand the effects of mammalian herbivory on New Zealand plants have accelerated in the last century and these efforts are beginning to paint an accurate picture of the scope of their detrimental effects. A wide range of mammalian herbivores, such as brushtail possums (*Trichosurus vulpecula*; Nugent *et al.* 2002; Sweetapple *et al.* 2002; Cochrane *et al.* 2003; Wilson *et al.* 2003; Sweetapple *et al.* 2004; Urlich & Brady 2005; Forsyth & Parkes 2005), deer (Husheer & Frampton 2005; Husheer *et al.* 2005; Wilson *et al.* 2006), domestic livestock (Mark & Dickinson 2003; Miller & Wells 2003; Walker *et al.* 2003; Smale *et al.* 2005) and rodents (Wilson *et al.* 2003; Wilson *et al.* 2006) can have strong effects on New Zealand forests. However, more long term studies are required to fully elucidate the implications of introduced mammals on New Zealand forests.

The location of KWS is advantageous for several reasons. It is close to a major metropolitan area to facilitate public outreach and education programs. It also contains several small reservoirs, which provide habitat for threatened water birds (e.g. brown teal, *Anas chlorotis*). However, the site also has several drawbacks. The forest within the reserve was cleared for farming in the mid 19th century and was subsequently abandoned at the turn of the century. It is therefore still undergoing succession and presently supports closed-canopy, broadleaf forest with a dense understory of tree ferns, vines and shrubs, but few canopy emergent trees. Before agricultural practices were abandoned, much of the area was planted with radiata pine (*Pinus radiata*), which persists to the present day. These pines were not removed prior to the initiation of the sanctuary, primarily for financial reasons. Instead, a management plan was developed that calls for the suppression of pine recruitment and the facilitation of native forest regeneration under the adult pines, which tower above the native bush. Therefore, native forest is slowly replacing the existing pine forest as the adult pines succumb to mortality naturally.

North-temperate pines can significantly alter the light and soil environment beneath their canopies (Pakeman *et al.* 2006; Iason *et al.* 2005). Soil chemistry studies in New Zealand have specifically shown that radiata pine depletes the availability of nitrogen and organic carbon in mineral soil, and increases soil acidity and surface leaf litter accumulation (Parfitt *et al.* 1997; Groenendijk *et al.* 2002). Some native plant species could be quite sensitive to these environmental changes, which may pose a problem for ecological restoration efforts. Pine plantations are commonplace globally (Aston *et al.* 1998; Zerbe 2002; van Wesenbeeck *et al.* 2003; Arévalo & Fernández-Palacios 2005a; 2005b) and can significantly alter the trajectory of native forest regeneration (Geldenhuys 1997; Dzwonko 2001). Radiata pine covers massive tracts of the New Zealand landscape (Nagashima et al. 2001, 2002, 2003). Although the distribution of native plants has been documented in pine plantations in several regions of New Zealand (McQueen 1961, 1973; Allen *et al.* 1995a, 1995b; Ogden *et al.* 1997), the effect of radiata pine on native forest regeneration is incompletely understood.

Just before mammal eradication and fence construction at KWS, we established several permanent plots to facilitate long term monitoring of forest succession. One plot was erected under a dense canopy of radiata pine and

another was established in a similar area devoid of pines. Within each 525 m^2 plot, we quantified the abundance, species richness and species composition of three size classes of all native woody plants. Here, we present a comparison of inventories made both before and a decade after the construction of the fence. Data are used to determine whether plant abundances, species richness and species composition have changed following mammal eradication and whether these changes differ among plots and plant size classes.

Methods

Study site

All data were collected at the southern tip of the North Island of New Zealand (41°18.3' S, 174°44.8' E), in the Karori Wildlife Sanctuary (KWS). The area experiences a mild, temperate climate, with annual rainfall averaging 127 cm and cloud cover obscuring the sun 54% of daylight hours (NIWA 2006). Elevation varies between 160 and 380 m. The vegetation is classified as coastal broadleaf-conifer forest (Dawson 1988; Wardle 2002), which is dominated by broadleaf evergreen trees, such as mähoe (*Melicytus ramiflorus*), five finger (*Pseudopanax arboreus*) and pate (*Schefflera digitata*; nomenclature follows Allan 1961; Connor & Edgar 1987; Webb et al. 1988). Tree ferns (*Cyathea* spp.) and shrubs such as hangehange (*Geniostoma rupestre*) and kawakawa (*Macropiper excelsum*) are common in the forest understory. Radiata pine occupy parts of KWS with many dominant trees greater than 25 m emerging well beyond the canopy of regenerating native forest. Moles & Drake (1999) and Campbell-Hunt (2002) provide more detailed descriptions of KWS.

Permanent forest plots

In 1995, a predator-proof fence was erected around the boarders of KWS and all fifteen introduced mammals have been actively excluded within ever since. Eight resident mammal species have been actively removed. These include the ship rat (*Rattus rattus*), mouse (*Mus musculus*), cat (*Felis catus*), stoat (*Mustela erminea*), hedgehog (*Erinaceus europaeus*), rabbit (*Oryctolagus cuniculus*), hare (*Lepus europaeus occidentalis*), and brushtail possum. A further seven species common to this area were also removed, including ferrets (*M. furo*), fallow deer (*Cervus dama*), goats (*Capra hircus*), pigs (*Sus domestica*), cattle (*Bos taurus*), Norway rats (*R. norvegicus*) and weasels (*M. nivalis*). On-going monitoring and control continue to exclude all introduced mammals from within the 8.6 km fence perimeter. See www.sanctuary.org.nz for further information on monitoring and control of pests at KWS.

Prior to fence construction and mammal eradication, two permanent forest plots were established in areas with similar abiotic environmental conditions. Plots were located on opposite sides of Kaiwharawhara stream, which flows in an east-west direction. The pine forest plot in KWS is located on the south side of the river and faces a northerly direction. The native forest plot is located on the opposite side of the river and faces a southeast direction. Both plots have similar slope angles (10 - 15°). To test for potential differences in soil moisture content, we collected 50 ml soil samples from 20 random locations one day after moderate rainfall from each plot during February 2006. Comparisons of their wet and dry weights failed to detect a significant difference in soil water

content between plots ($F_{1, 18}$ = 1.136, P = 0.301).

Both plots were similarly constructed. Each encompassed a total of 525 m^2 of forest (35 x 15 m), which was subdivided into 5 x 5 m smaller plots with permanent metal stakes. All woody plants located within plot boundaries that were greater than 5 m tall ('adults' from hereafter) were identified and permanently marked with metal tags. All woody plants between 0.4 and 5.0 m tall ('poles' from hereafter) were counted within ten, randomly chosen 5 x 5 m subplots, leading to a total of 250 m^2 of sampling area for the 'pole' size class. All woody plants between 0.05 and 0.4 m tall ('seedlings' from hereafter) were counted in 1 x 5 m strips within each subplot, leading to a total of 50 m^2 of sampling area in each plot for the 'seedling' size class. As a result, each life history stage was censused over different areas, which were chosen to correspond with ontogenetic changes in plant stature and density. In December 2005, 10 years after the first census in 1995, each plot was re-censused using the same protocol.

Two 0.05 ha plots within a 252 ha reserve is a modest representation of the plant community. However, the plots encompass both types of forest present in the reserve and over 3,800 plants were encountered during sampling. Therefore, inventories from the plots provide a useful description of successional changes following mammal eradication.

Analyses

We conducted three separate analyses to test for differences in tree abundance and diversity between forest plots and sampling times. We used repeated measures analysis of variance to evaluate potential changes in tree abundances (SPSS 2002). We chose this test to account for the independence problem associated with repeatedly sampling each plot. The total number of trees from each species was used as the dependent variable. Sampling time (before and after pest eradication) was treated as a repeated measure. Forest plot (pine and native) was considered a fixed-factor. We assessed the independent effect of sampling time to determine whether overall plant abundances changed after mammal eradication. We also assessed the interaction between sampling time and plot, to determine whether successional changes were similar between plots. Separate analyses were conducted for each life history stage (seedlings, poles and adults). To promote normality and homoscedasticity by reducing the number of zeros in the dataset, we restricted our attention to common species that were encountered more than five times (Table 1). Abundances of all three life history stages were $\log_{10}$ transformed prior to analyses to conform to assumptions.

We used rarefaction (Sanders 1968) to test for differences in species richness between plots and sampling times. Estimates of species richness on a per area basis can be confounded population density, because the number of species encountered during sampling typically increases with the number individuals censused (Gotelli & Graves 1996; Gotelli & Colwell 2001). Rarefaction accounts for the confounding effect of population density by measuring species diversity on a per-individual, rather than a per-area, basis. Species richness was estimated by randomly selecting different numbers of individuals from the total pool of individuals encountered during sampling using a computer simulation, and plotting changes in cumulative species richness as a function of the total number of

individuals sampled. The average number of species randomly sampled from a given number of individuals was then compared between plots and sampling times. Species richness was rarefied to the smallest number of plants found across forest plots and sampling times for each life history stage separately. Instead of calculating 95% confidence intervals for average rarefied richness values, we calculated 99% confidence intervals to facilitate multiple comparisons (i.e. control for experiment-wide error). Comparisons were made between forest plots within each sampling time, and between sampling times within forest plots, leading to a total of four comparisons with each life history stage. Samples with non-overlapping confidence intervals were considered statistically different. All rarefaction analyses were conducted using *Analytic rarefaction 1.3* (Holland 2003).

Differences in species composition were assessed with PROXSCAL non-metric multi-dimensional scaling (NMDS). NMDS is a multivariate procedure that represents a symmetrical data matrix as a series of points in two dimensional, Euclidean space (Borg & Groenen 1997). Euclidian distances between points generated by NMDS correspond to overall differences in matrix inputs. We conducted the analysis in SPSS (2002) on a single matrix consisting of tree species (including rare ones) entered as rows, and life history stages (seedlings, poles and adults) entered as columns. Separate columns were created for each forest plot and census time, leading to a total of 12 columns and 12 corresponding multi-dimensional data points. Entries in the matrix were the total number of plants from all 22 tree species that were encountered in each condition. Points generated by NMDS that are separated by small Euclidian distances represent similar species composition, while distantly separated points represent different species composition.

Results

Changes in tree abundances were observed between sampling times (Figure 1). However, these changes differed between life history stages. Seedlings increased in abundance between sampling times ($F_{1,28} = 12.688$, $P = 0.001$) and these changes did not differ between plots ($F_{1,28} = 1.100$, $P = 0.303$). Poles increased in abundance between sampling times ($F_{1,28} = 20.165$, $P < 0.001$) and these changes did not differ between plots ($F_{1,28} = 0.008$, $P = 0.929$). Adults declined in abundance between sampling times ($F_{1,28} = 15.772$, $P < 0.001$) and these changes did not differ between plots ($F_{1,28} = 1.640$, $P = 0.221$).

Few differences in species richness were observed between census times and

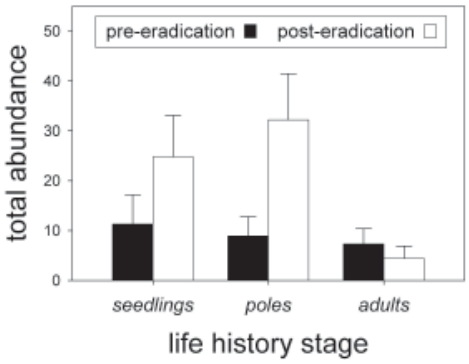

Figure 1. Average abundance (± se) of seedlings (0.05 - 0.4 m tall), poles (0.4 - 5.0 m tall) and adults (> 5.0 m tall) of 15 common tree species in the Karori Wildlife Sanctuary, both before (closed bars) and after (open bars) mammal eradication. Changes in abundance were similar in both forest plots (see text).

forest plots (Figure 2). Nine out of 12 total comparisons failed to detect differences in species richness. Three differences were observed; one comparison involved adult trees, the other two involved seedlings. First, species richness of adult trees in the native forest plot was higher before mammal eradication than after eradication. Second, species richness of seedlings in the pine-dominated plot increased after mammal eradication. Third, prior to eradication, seedling species richness was higher in the pine forest plot than in native forest plot.

Tree species composition differed markedly between censuses and plots. Normalized raw stress generated by the multidimensional scaling was 0.0148, indicating that multivariate differences between groupings could be accurately represented in two dimensions (Borg & Groenen 1997). The first dimension generated by NMDS clearly differentiated the two forest plots, with pine forest having higher values than native forest (Figure 3). The second dimension differentiated seedlings and poles between sampling periods, with the post-eradication census generating greater values than the pre-eradication census. However, the second dimension failed to differentiate adults, indicating this life

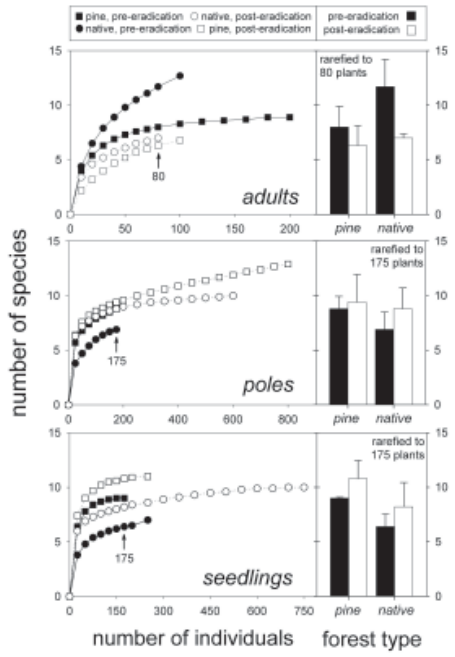

Figure 2. Species richness of adults (> 5.0 m tall, top), poles (0.4 - 5.0 m tall, middle) and seedlings (0.05 - 0.4 m tall, bottom) of 22 tree species in the Karori Wildlife Sanctuary. At left are rarefaction curves representing the number of species found per individual encountered in both the pine forest plot (squares) and the native forest plot (circles), before (closed symbols) and after (open symbols) mammal eradication. At right are average values of species richness (± 99% confidence intervals) rarefied to a constant number of individuals (80 adults, 175 poles and seedlings), both before (closed symbols) and after (open symbols) pest eradication in both forest plots.

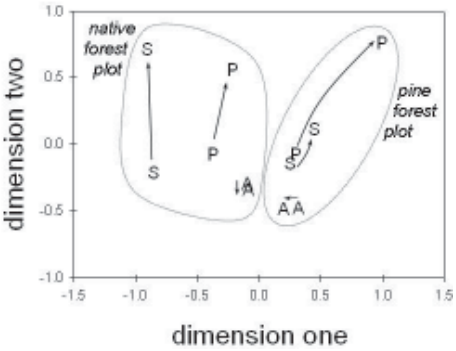

Figure 3. Multidimensional scaling of the species composition of seedlings (0.05 – 0.4 m, 'S'), poles (0.4 - 5.0 m, 'P') and adults (> 5.0 m, 'A') of 22 tree species. Two sampling periods (before and after mammal eradication) are connected by arrows, which point to later sampling dates. Dashed circles unite data points collected in either the pine forest plot (right) or the native forest plot (left).

Table 1 Total abundance of the 22 common tree species in the Karori Wildlife Sanctuary plots. Separate values are listed for three life history stages (seedlings, poles and adults), two forest plots (pine-dominated and native-dominated) and two sampling times (before and after pest eradication).

	Pre-eradication						Post-eradication					
	Native			Pine			Native			Pine		
	Seedlings	Poles	Adults	Seedlings	Poles	Adults	Seedlings	Poles	Adults	Seedlings	Poles	Adult
Alectryon excelsus	29	13	6	0	0	0	99	92	3	0	0	0
Aristotelia serrata	0	0	0	13	0	8	0	0	0	12	12	2
Brachyglottis repanda	0	0	0	14	44	14	0	0	0	36	210	0
Coprosma grandifolia	0	0	0	15	8	12	0	0	0	11	63	1
Corynocarpus laevigatus	6	147	3	0	0	0	223	116	3	0	0	0
Dysoxylem spectabile	250	24	61	0	0	0	240	113	52	0	0	0
Eleaocarpus dentatus	0	0	0	0	0	0	2	0	0	0	0	0
Fuchsia excorticata	0	0	1	0	0	0	0	0	0	0	0	0
Geniostoma rupestre	2	0	8	62	47	5	44	143	0	146	263	4
Hedycarya arborea	8	1	2	0	0	0	38	0	1	3	4	0
Hoheria populnea	0	0	1	0	0	1	0	9	0	0	1	0
Knightia excelsa	0	0	0	0	0	0	2	1	0	3	0	0
Laurelia novae-zelandiae	0	0	1	0	0	0	0	3	1	0	0	0
Macropiper excelsum	17	2	13	4	5	0	97	18	12	23	41	0
Melicytus ramiflorus	0	2	8	4	35	120	14	78	9	51	148	98
Myrsine australis	1	0	0	2	1	0	0	0	0	6	1	0
Olearea rani	0	0	2	0	3	0	0	0	0	0	0	0
Pinus radiata	0	0	0	0	0	11	0	0	0	0	0	4
Pittosporum eugeniodes	0	0	0	0	0	0	0	0	0	0	1	0
Pseudopanax arboreus	0	0	1	62	29	37	0	0	0	24	50	3
Schefflera digitata	0	3	2	7	1	3	2	8	0	7	20	0
Sophora microphylla	0	0	0	0	0	0	0	0	0	0	1	0

history stage maintained similar species composition through time.

Common tree species could be qualitatively assigned into several categories of distribution (Table 1). *Alectryon excelsus, Corynocarpus laevigatus and Dysoxylem spectabile* were only found in the native forest plot. Conversely, *Aristotelia serrata, Brachyglottis repanda* and *Coprosma grandifolia* were only found in the pine forest plot. All six of these species also increased in abundance after mammal eradication. *Geniostoma rupestre*, *Melicytus ramiflorus*, and *Schefflera digitata* increased in abundance after mammal eradication. Two common species were more difficult to categorize. *Pseudopanax arboreus* was more abundant in the pine forest plot and declined in abundance after mammal eradication. *Hedycarya arborea* was restricted to the native forest plot before mammal eradication, but colonised the pine forest plot afterward.

Discussion

Several components of tree diversity differed between forest plots and census times. Although abundances of adult trees remained largely unchanged between censuses, seedlings and poles increased in abundance after mammal eradication. No consistent trends in tree species richness were observed, both through time and between forest plots. Strong differences in species composition were observed, although both plots showed similar changes in the species composition of seedlings and poles following mammal eradication.

Increases in the abundance of seedlings and poles suggest that browsing by introduced mammals may suppress abundances of smaller, younger plants. Similar results have been found by other studies investigating the effects of introduced mammals on native New Zealand forests (Nugent *et al.* 2002; Husheer *et al.* 2005; Wilson *et al.* 2006). A related explanation could be that reintroduction of native seed dispersers has accelerated the process of plant recruitment. Prior to the construction of the fence, abundances of most avian seed dispersers were much lower than they are presently (C. Miskelly, unpublished data). Therefore, plant densities could have been constrained by seed limitation and the increasing abundances of smaller-sized plants may be the product of enhanced dispersal efficiency. Changes in abundances could also result from other types of successional processes. For example, at the current stage of succession, canopy tree species such as *Pseudopanax arboreus* have reached maturity and may be at the early stages of self-thinning (Pretzsch 2006). Tree mortality resulting from self-thinning may allow more light to reach the forest floor, which in turn might stimulate the germination, growth and survivorship of seedlings.

We failed to observe strong differences in species richness, both between forest plots and sampling times. After controlling for variation in tree abundances, only three differences were observed. First, species richness of adult trees declined in the native forest plot through time. This change was concomitant with the plot extinction of six tree species (*Fuchsia excorticata*, *Geniostoma rupestre, Hoheria populnea, Olearea rani*, *Pseudopanax arboreus* and *Schefflera digitata*). All six of these species are relatively small in stature and could be considered early successional species. Therefore, they might be in the process of replacement by larger species such as *Dysoxylem spectabile*. Second, species richness of seedlings was initially higher in pine forest than in native forest.

Several factors may be important. The pine plot contained three more tree species than the native forest plot. The native forest plot was also dominated by *Dysoxylem spectabile*, which is one of the most common trees in the reserve, but was never encountered in the pine plot. Its dominance in the native forest plot may promote reduced species richness, when quantified on a per individual basis. Third, seedling species richness in the pine forest plot increased after pest eradication. Two species, *Hedycarya arborea* and *Knightia excelsa*, colonized the plot during this time. Although the cause of this change is difficult to pinpoint, their expansion into the pine-dominated plot may be due to the relaxation of mammalian browsing.

Strong differences in species composition were observed not only between plots but also through time. Six species were found only in the pine forest plot and another six species were found exclusively in the native forest plot. Nevertheless, both plots showed similar changes in species composition through time. Changes in species composition resulted mostly from similar increases in *Geniostoma rupestre*, *Macropiper excelsum* and *Melicytus ramiflorus* in both plots. This result indicates that the management plan for introduced pines is achieving its goals.

The increase in abundance of seedlings and saplings suggests introduced mammals may suppress the abundance of smaller, younger plants. Previous work has typically focused on the effects of particular pest species. For example, the effects of brushtail possum on the foliage, growth and regeneration of *Fuchsia excorticata* (Urlich and Brady 2005), *Dysoxylum spectabile* (Nugent *et al* 2002) and *Melicytus ramiflorus* (Forsyth and Parkes 2005) has been documented. Similarly, red deer (*Cervus elephus*) suppress the growth and regeneration of *Coporosma grandifolia* (Husheer *et al* 2005), and the Norway rat (*Rattus norvegicus*) limits the dispersal of *Schefflera digitata* seeds (Allen and Lee 1994). The combined effects of all introduced mammals are less frequently documented (e.g. Fitzgerald and Gibb 2001). Additional studies of vegetation change in mainland islands before and after pest eradication will help bridge this gap.

Complex changes in forest structure have occurred since in the Karori Wildlife Sanctuary in the decade following the construction of the fence and the exclusion of introduced mammals. Long-term monitoring in two permanent forest plots has shown that the abundance of smaller plants has increased. Although both plots have experienced similar changes in species composition, few changes in species richness were observed. Overall results therefore indicate that different components of plant diversity can change independently following the exclusion of mammals and the reintroduction of native birds into predator-free 'mainland islands'.

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